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THE REACTION OF WHEAT VARIETIES AT TWO STAGES OF MATURITY TO SIXTEEN PHYSIOLOGIC FORMS OF *PUCCINIA GRAMINIS TRITICI*.*

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It has been pointed out by several investigators, Aamodt (*1*); Hayes, Stakman and Aamodt (*6*); Goulden, Neatby and Welsh (*3*); Neatby and Goulden (*8*), and Goulden (*2*), that some varieties of wheat show a striking difference between their reactions to the stem rust organism in the seedling and mature plant stages. This was first observed in the field. It was noticed that certain varieties, while susceptible to some physiologic forms in the seedling stage, were resistant in the field, regardless of the forms present. It was evident, either that seedling resistance increased as the plants approached maturity or that another and perhaps quite different type of resistance developed. The latter possibility was indicated in the observations made by Hursh (*7*), on the morphology of such varieties as Kota and Acme which exhibited greater resistance in the field than in the seedling stage. More recently Hart (*5*) has shown that some of these varieties vary in the time of opening of the stomata. The varieties showing field resistance do not appear to open their stomata until after the morning dew has disappeared, and consequently germinating rust spores are killed before the infection hyphae have an opportunity of passing through the open stomata. This type of resistance is described as "functional resistance". Previously Goulden, Neatby and Welsh (*3*), Neatby and Goulden (*8*) and Goulden (*2*), had shown that mature plant resistance in H-44-24 X Marquis crosses and in a Pentad X Marquis cross was inherited in a very simple manner. This suggests a certain degree of simplicity in the nature of mature plant resistance and lends support to the theory of its functional nature. The same writers showed that mature plant resistance was inherited entirely independently of the physiological resistance observed in the seedling stage. This is a further indication of a sharp distinction between the nature of the two types of resistance.

Harrington and Smith (*4*) studied the seedling and mature plant reactions of four varieties, Marquis, Marquillo, Iumillo, and Vernal to three physiologic forms 17, 21, and 36. In addition to the four varieties they used a susceptible strain of Marquillo and a susceptible strain of Iumillo. A good agreement was obtained between the reactions in both stages with the exception that the susceptible strain of Iumillo seemed to be more resistant in the after heading stage. However, the material used by these writers was probably not sufficiently varied to give them a clear indication of mature plant resistance.

Since two types of resistance exist, in the breeding of rust resistant varieties, it is expedient to know the reaction of varieties used as parents in

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the two stages of development. Some varieties may possess only seedling resistance. Others may possess only mature plant resistance, and still others may possess both. A fairly complete knowledge of the behaviour of parent varieties would be of great assistance in breeding work, especially since we know that in at least two crosses the inheritance of the two types is independent. A further consideration is the relative importance of the two types of resistance from a practical standpoint. If the mature type of resistance is due to the structure, or to the functional behaviour of the plant, it seems reasonable to expect that it should apply equally to all physiologic forms since they are are differentiated by their reactions on different host varieties in the seedling stage. If such is the case, the mature plant type of resistance is of great practical importance. The multiplicity of physiologic forms, and the possibility of their increase by hybridization and mutation is alarming if the plant breeder has to utilize seedling resistance only. But if mature plant resistance applies almost equally to all forms, and is fairly simple in inheritance, it is of much more practical importance from the breeding standpoint.

In order to obtain more information on some of the above points the authors outlined, in 1927, a definite project for the purpose of studying the mature plant reactions of 14 wheat varieties to at least 16 physiologic forms. This work was completed during the winter of 1928-29 and the results are reported here.

Materials and Methods

The varieties selected for the rust resistance tests were mainly those being used in crosses in progress at the Dominion Rust Research Laboratory. The names of these varieties are, Reward, Marquis, Quality, Kota, Marquillo, Garnet, H-44-24, Hope, Vernal emmer, Acme, Pentad, Iumillo, Black Persian and Khapli. This makes a very interesting group for such a study, as it includes such varieties of *T. vulgare* as Marquis, Reward, Garnet and Quality, which are ordinarily quite severely damaged by rust, and others, such as Marquillo, Kota, H-44-24 and Hope, which are also vulgare varieties, but are highly resistant,—at least under field conditions. The other varieties all belong to the Emmer or 28 chromosome group and are nearly all highly resistant. Results of tests of the rust resistance of all of these varieties in the seedling stage have been given by Newton and Johnson (*9*), and Newton, Johnson and Brown (*10*); and these are the results which have been utilized in the present study for comparison with the mature plant reactions.

The plants studied for mature plant reactions were grown in a cool section of the greenhouse until the heads protruded about four or five inches beyond the uppermost sheath. It was found, that if inoculations were made at a more advanced stage infections were less successful. Three different methods of inoculation were tried, but only one found satisfactory. By the first method, the plants were sprayed with a spore suspension of the forms to which they were to be tested, but as the plants did not always become uniformly rusted this method was discontinued. Inoculations by means of the ordinary flat inoculating needle were tried next, and proved to be fairly satisfactory. This method, however, had one disadvantage. A slight amount

of needle injury was liable to occur, and at the time of reading the rust reactions this injury could not be distinguished from chlorotic and necrotic areas due both to rust, and to adverse environmental conditions. A few wheat varieties, in the adult stage, tend to fleck and to develop chlorotic and necrotic areas after they have been incubated in an atmosphere of high humidity, even when no rust has been applied. The method, therefore, which was finally adopted and one which gave fairly uniform results, was that of inoculating the plants by means of the fingers. The bloom was removed from the stems and leaves of all plants by gently rubbing them with the moistened fingers. Then the inoculum was applied by the fingers to all parts of the stems and leaves. After inoculation, the plants were placed in tall incubation chambers lined with blotting paper to increase the humidity, and were left there for two days. At the end of this period they were removed from the chambers, and kept subsequently, in a section of the greenhouse which was maintained at a temperature of about 70°F. during the daytime. About three weeks were necessary for complete rust development. In most varieties, the infection became progressively heavier until the plants began to ripen, and the rust passed into the telial stage. Consequently, it was found most satisfactory to read the reactions at a definite time after removal from the incubation chambers. Duplicate tests were made of each variety, each test being made with one pot of three to five plants.

The reading of mature plant reactions was a very difficult task, owing to the extreme variation in resistance on different plants. There was also great variation in the reaction types exhibited by different varieties. A variety such as Khapli will often show a large number of very small pustules, while another, such as Hope, will show a much smaller number of relatively large pustules. To obtain a complete record, the plant was divided into four regions, upper and lower culms, and upper and lower leaves. The lower part of the plant consisted arbitrarily of about the lower one third. Readings were taken first on the basis of pustule size on the four regions of the plant. The notation 0, (;), 1—, 1, 1+, 2—, 2, 2+, 3—, 3, 3+, 4—, 4, 4+, which corresponds with that used for reading seedling reactions, was used to indicate pustule size. Much less attention was paid to chlorosis and necrosis when marking adult plants than when marking seedling plants, as it was observed that on the leaves of mature plants chlorosis was quite definite even on susceptible plants, and very often definite on the leaf sheaths also. It was felt that this did not indicate resistance in the same sense as it does in the seedling stage, and that the best procedure would be to consider size of pustules chiefly. In addition to the readings of pustule size on the different regions of the plant, notes were taken on the percentage of infection on the whole plant. This was found to be very useful, as it served to differentiate between varieties which were quite susceptible, and those which showed uniformly a small number of quite large pustules.

A small specimen of the greenhouse record sheet, shown in table 1 will indicate how the notes on pustule size were taken. In addition to this, a margin on the sheet was left for notes and comments. It will be noted

that to form 15, the pustule size, on the upper leaves of Vernal, was recorded as (3 4). This means that the pustules ranged in size from 3 to 4 with type 3 predominant.

TABLE 1. *Specimen of greenhouse record sheet showing method of recording mature plant reactions.*

Variety-Vernal

	Pot 1		*Pot II-Duplicate*	
Form	Leaves	Culms	Leaves	Culms
38	Upper (;) Lower (;)	Upper (1) Lower (;)	Upper (;) Lower (;)	Upper (0) Lower (1−)
15	Upper (3 4) Lower (3)	Upper (3 4) Lower (3+)	Upper (3 4) Lower (3)	Upper (3 4) Lower (3+)

In order to summarize the data obtained, an attempt was made to give numerical values to the rust reactions. For seedling reactions this was comparatively easy. The numerical values assigned to the rust reaction classes are given in table 2.

TABLE 2. *Numerical values arbitrarily assigned to rust reaction classes.*

Rust reaction	0	0;	1=	1−	1	1+	1±	1++	2=	2−	2±	2+	2++	3=	3−	3	3±	3+	3++	4=	4−	4	4+	4++
Numerical value	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24

In addition to these classes some of the varieties show the so-called X reactions in the seedling stage. Since an X-reaction fluctuates from the resistant to the susceptible class, it has been given the arbitrary value of 2++ to 3, that is X− = 13, X = 14, X+ = 15, X++ = 16.

It will be obvious from an inspection of table 1 that it was somewhat more difficult to assign numerical values to mature plant reactions. A somewhat similar system, however, was employed with the exception that averages were computed, based on the range in pustule size. Thus in table 1 the reaction of Vernal emmer varies from 0; to 1— but since 0; = 2, and 1— = 4, the average reading is the average of 2 and 4 = 3. To form 15 it will be noted that pustule size ranges from 3 to 4 with the 3 pustule type predominating in every case. In general the predominating type of pustule was taken as a measure of the rust reaction as in most cases the second type of pustule was comparatively rare. In cases where most of the readings were 3 to 4 the range would be taken as 3 to 3+. Therefore for Vernal to form 15 the range would be taken either as 3 to 3+ or 3 to 3++ giving an average reading of 18 or 18.5. This method appeared to give quite consistent results, and, when a number of the estimates were repeated, values within ½ or 1 point of the original values were obtained.

The system outlined above, was followed in the preparation of table 3. This table shows the numerical values for the reactions of all the varieties to 16 forms. Percentages are also recorded in this table. In our notation for percentages, 1% represents the amount of rust which is ordinarily indicated by a "trace".

TABLE 3. *Seedling reactions, mature plant reactions, and percentages of rust obtained in tests of 14 varieties of wheat to 16 physiologic forms.*

Variety		9	14	15	17	19	21	32	33	34	36	38	48	49	50	52	53	Average	
Garnet	Seed. react.	22	22	23	23	23	23	17	23	23	23	23	23	23	24	23	23	22.69	
	Mat. react.	23	23	23	23	23	21	23	23	21	23	23	23	24	22	23	23	22.75	− .06
	% Rust	87	60	80	80	80	80	40	80	80	80	80	80	85	65	75	65	74.8	
Marquis	Seed. React.	22	10	22	22	10	23	21	11	22	23	9	5	22	13	23	12	16.88	
	Mat. React.	23	9	21	23	11	21	18	12	21	23	8	7	23	11	22	10	16.45	+ .43
	% Rust	67	10	72	85	40	55	45	30	70	57	45	45	77	60	77	60	55.9	
Quality	Seed. React.	22	11	23	22	13	19	19	13	22	19	11	10	23	18	19	7	16.94	
	Mat. React.	21.5	8	24	21.5	8	21	20.5	11	23	21.5	11	12	20.5	20	20	10	17.09	− .15
	% Rust	87	70	85	85	25	80	70	20	80	80	32	20	72	70	80	20	61.0	
Reward	Seed. React.	19	13	22	17	18	22	17	13	22	17	13	17	19	18	19	13	17.56	
	Mat. React.	14	6	15	18	18	12	15	13	20	14	15	8	23	18	14	9	14.50	+ 3.06
	% Rust	70	60	65	55	50	70	60	75	75	35	5	30	70	80	70	20	55.6	
Marquillo	Seed. React.	18	2	18	18	5	12	16	2	18	18	12	12	13	19	18	10	13.19	
	Mat. React.	11	2	14	11	4.5	11	14	3	10	15	8	7	9	17	8	9	9.59	+ 3.60
	% Rust	40	1	55	30	1	25	40	1	10	40	10	5	30	30	10	12	21.2	
Kota	Seed. React.	20	8	20	19	16	20	19	7	21	20	16	7	21	13	23	5	15.94	
	Mat. React.	14	7.5	14	15	14	20	15	7.5	15	14	10.5	6	14	14	17	4.5	12.62	+ 3.32
	% Rust	42	15	45	60	40	50	60	2.5	60	40	30	1	65	20	30	10	35.66	
H-44-24	Seed. React.	18	11	18	18	7	18	16	5	18	5	13	18	5	5	7	13	12.19	
	Mat. React.	4	2	4.5	4	2.5	6.	4	3	10	3	3.5	10.5	2.5	3	3	7	4.53	+ 7.66
	% Rust	5	0	12	5	2.5	5	1	1	10	1	1	10	5	1	5	1	4.1	
Hope	Seed. React.	16	7	18	17	11	19	17	5	19	5	7	7	2	2	10	11	10.81	
	Mat. React.	7.5	3	6	6	7.5	4.5	6	3	6	3	6	2	3	3	2	3.5	4.50	+ 6.31
	% Rust	10	1	15	5	1	5	2.5	.5	10	5	1	10	1	1	1	1	4.4	
Acme	Seed. React.	20	20	20	20	20	20	15	20	20	20	16	22	19	15	23	23	19.56	
	Mat. React.	6	4	11	7	3	10	3.5	4	9	4	4.5	14	4.5	7	3	14	6.78	+12.78
	% Rust	5	1	1	5	1	22	1	1	5	5	5	15	1	5	1	5	4.9	
Vernal	Seed. React.	21	3	21	3	2	2	3	4	2	2	3	3	2	2	24	18	7.19	
	Mat. React.	18	3	18	3	3.5	3.5	2	2	2	2	3	2	1	2	19	23	6.69	+ .50
	% Rust	30	1	30	1	1	1	0	0	0	0	1	0	1	0	50	45	10.07	
Pentad	Seed. React.	16	18	12	18	18	18	2	13	23	2	6	2	14	7	2	19	11.88	
	Mat. React.	3	3.5	9	4	2	12	3	2	1	2	2	2	2	2	2	12	3.97	+ 7.91
	% Rust	5	1	5	1	1	25	1	0	0	0	1	0	0	1	1	7	3.08	
Black	Seed. React.	7	5	12	12	12	12	12	11	12	14	13	11	12	14	13	10	11.38	
Persian	Mat. React.	6.5	3.5	4.5	7.5	7.5	8.5	5	3	6.5	3.5	5.5	3.5	6.5	6	7.5	7.5	5.78	+ 5.60
	% Rust	1	1	1	5	5	5	1	1	1	50	5	1	5	10	45	2.5	8.72	
Khapli	Seed. React.	4	2	3	3	3	3	4	5	3	4	7	7	3	2	4	5	3.88	
	Mat. React.	4.5	3	4.5	3	3	4.5	3	3.5	3	4	3	3	3	3	3	3.5	3.40	+ .48
	% Rust	60	30	70	35	45	60	10	40	50	35	5	40	30	10	17	35	38.88	
Iumillo	Seed .React.	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2.0	
	Mat. React.	2	3	2	2	3	2	2	2	2	2	3	2	2	2	2	2	2.19	− .19
	%Rust	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	.31	

Figures 1 to 14 represent diagramatically the reactions in the seedling and mature plant stages of 14 varieties to 16 physiologic forms of *P. graminis tritici.* In each figure the black dots represent seedling reactions and the circles mature plant reactions.

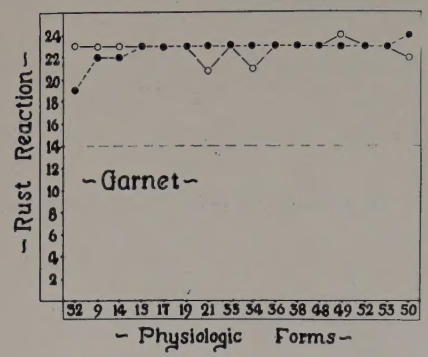


Figure 1

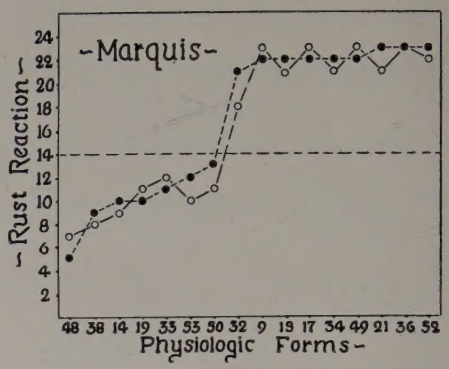
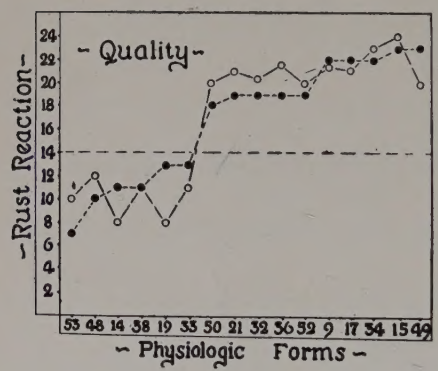


Figure 2



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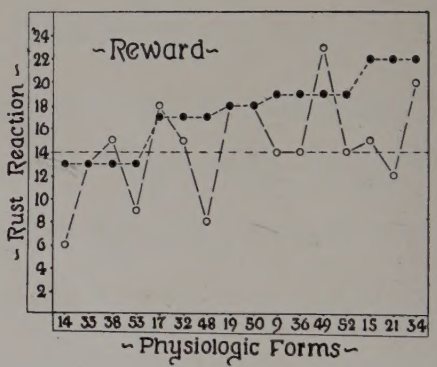

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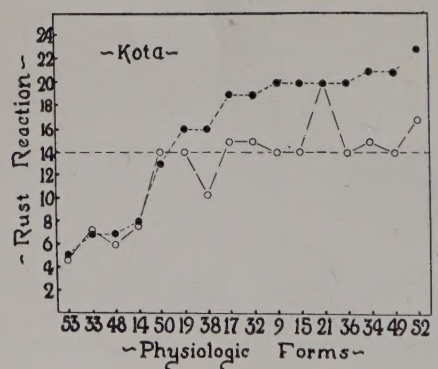

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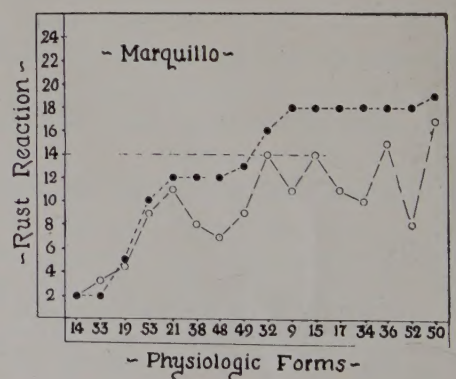

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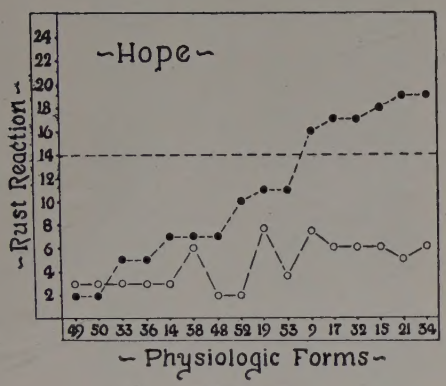

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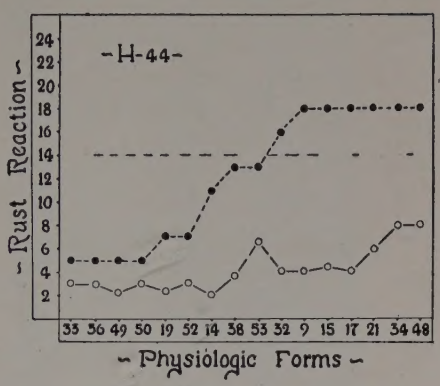

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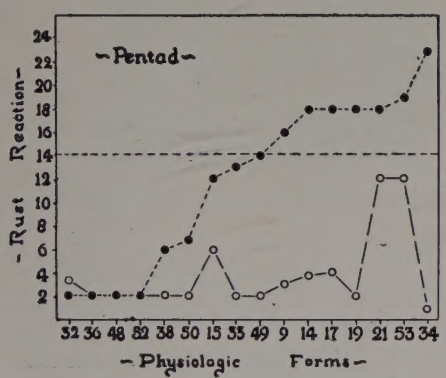

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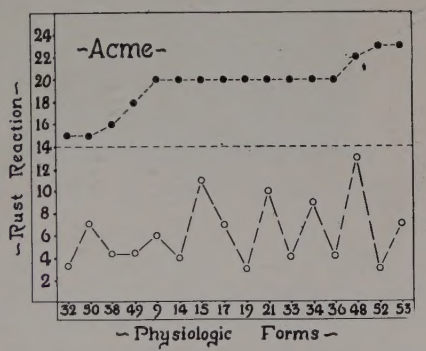

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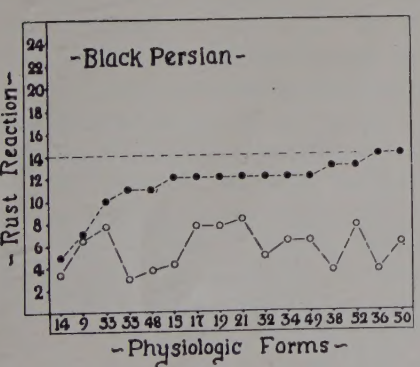


Figure 11

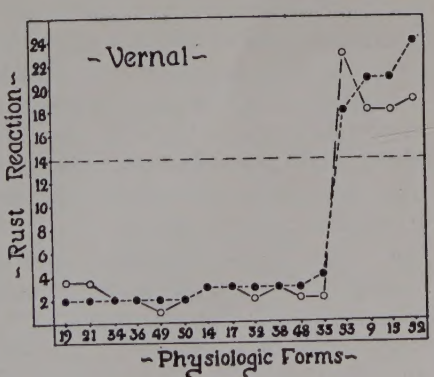
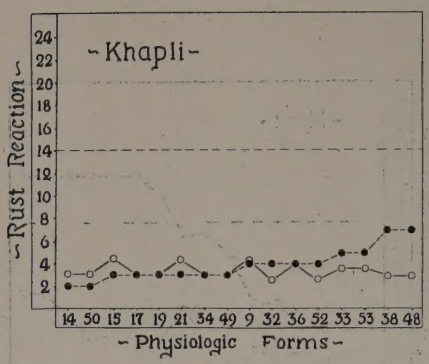


Figure 12



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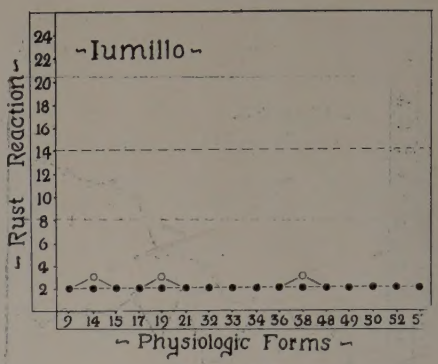

Figure 14

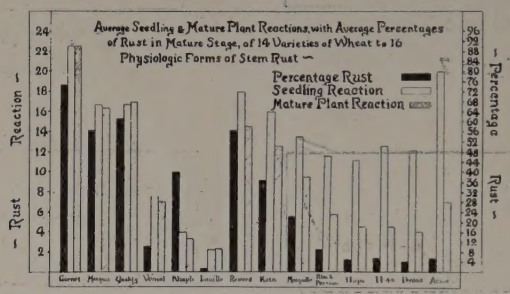
Average Seedling & Mature Plant Reactions, with Average Percentages of Rust in Mature Stage, of 14 Varieties of Wheat to 16 Physiologic Forms of Stem Rust -
Percentage Rust
Seedling Reaction
Mature Plant Reaction
- Rust Reaction -
- Percentage Rust -

Figure 15. Average seedling and mature plant reactions with average percentages of rust on mature stage of 14 varieties of wheat to 16 physiologic forms of stem rust.

Results and Analysis

Varietal Resistance

The mature plant and seedling reactions of each variety to the 16 physiologic forms are set forth in figures 1 to 14. The black dots represent the seedling reactions of the variety to the different physiologic forms. In order to make this more obvious to the eye the physiologic forms are arranged in order according to the reaction of the variety,—those to which the variety are more resistant are placed to the left and those to which it is more susceptible are placed to the right. Thus if a variety possesses high resistance to some forms, and moderate resistance and susceptibility to others, the line joining the black dots is roughly a diagonal one across the chart. Very susceptible varieties such as Garnet show a horizontal line at the top of the chart, while very resistant varieties such as Iumillo, show a horizontal line near the base of the chart. It should be noted that the immune class is represented numerically as 1 so that none of the points can be exactly on the base line. After the charts showing seedling resistance were set up, the circular dots were put in representing mature plant resistance. The charts when complete give, therefore, a fairly clear and complete picture of the reactions of each variety in both stages of growth.

The important feature brought out by these figures was the very close agreement between seedling and mature plant resistance in some varieties, and, in others, of the almost complete lack of agreement. In those lacking agreement, the varieties were much more resistant in the mature plant stage

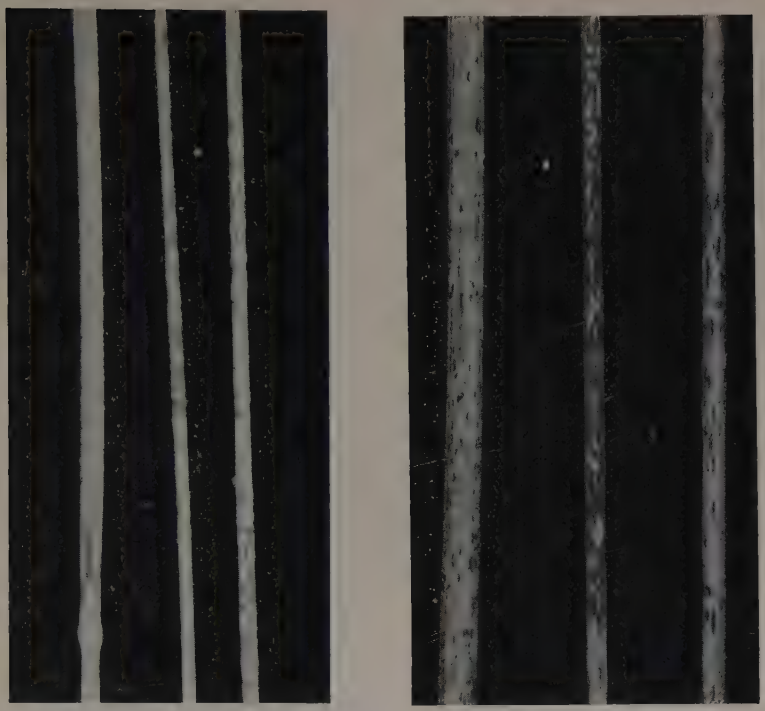

Figure 16. Reaction of stems of Quality wheat to form 38.

than in the seedling stage. On the basis of these results, it is possible to divide the varieties into fairly distinct groups. First we have the varieties that show no evidence of mature plant resistance. In this group we have Garnet, Marquis and Quality. The first of these shows no appreciable resistance to any of the forms used in either stage of growth, while Marquis and Quality show varying degrees of seedling resistance with corresponding mature plant reactions. In contrast to Garnet, Marquis, and Quality, we have such varieties as Acme, Pentad, H-44-24, and Hope that show a very decided lack of agreement between the seedling and mature plant reactions. Acme is the most striking in this respect, as while showing very little seedling resistance to any of the forms, it is resistant in the mature stage to all of them. The figures for Pentad, H-44-24, and Hope are somewhat similar, as these varieties show varying degrees of seedling resistance, and a fairly uniform degree of resistance to all forms in the mature stage.

Between the two contrasting groups, one showing mature plant resistance and the other none, are the remainder of the varieties, which are best considered individually.

Vernal emmer is highly resistant in the seedling stage to most of the forms, but it is quite susceptible to a few of them. There seems, moreover, to be a very good agreement between the reactions in the two stages. This does not agree particularly well with field observations, as Vernal emmer, in our experience, has never rusted heavily in the field, even when forms

were used in the artificially induced epidemic to which Vernal is susceptible in the seedling stage. A complication of this sort will probably not be fully explained until more is known about the exact nature of mature plant resistance in each variety, and its behaviour under different environmental conditions. There may be more than one type of mature plant resistance, and it is possible that one or other of these types is not fully expressed under greenhouse conditions. Some evidence of this seems to accrue from the results with Pentad. It will be noted from figure 9 that the mature plant reactions of Pentad to forms 21 and 53 are quite at variance with its reactions to the remainder of the forms. Obviously all of the tests could not be made under exactly similar conditions of temperature and sunlight and this may account for the quite different reactions obtained with these two forms. This seems especially likely if the Pentad resistance is of the functional or stomatal type, as temperature and sunlight may have a decided effect on the opening of the stomata.

An interesting fact concerning Vernal is brought out in table 3 by the rust percentages on the mature plants. Varieties such as Garnet and Marquis are not only susceptible to a number of forms in the seedling stage, but they also show a correspondingly high percentage of rust to these forms in the mature stage. With Vernal, however, the highest percentage is 50 per cent to form 52, and while this is very high compared with the 1 per cent and 0 per cent obtained to resistant forms, it is substantially less than that shown by Garnet or Marquis to forms to which they are susceptible in the seedling stage.

The varieties Reward, Kota, and Marquillo form a series with about the same degree of seedling resistance, and some indications of mature plant resistance. Reward shows the least mature plant resistance and Marquillo the most. In Reward the presence of mature plant resistance is, in fact, rather doubtful. In Kota and Marquillo, as indicated by their reactions, the presence of mature plant resistance is much more marked but it is not as marked as in Hope, H-44-24 and Pentad.

Black Persian shows some seedling resistance to all of the forms, but its mature plant reactions indicate considerably higher resistance. This is an indication that mature plant resistance is also present, and there is just sufficient seedling susceptibility to enable this to be detected by a comparison of the tests.

Iumillo presents a quite different appearance to Black Persian. It is resistant in the seedling stage to all of the forms used. The mature plant reactions, therefore, correspond perfectly with the seedling reactions, and, if an additional resistance appears in the mature plant stage, it cannot be detected.

Khapli gave results very similar to what would be expected from field observations. Resistance is very high in all forms in both stages. The points in the figure representing the seedling reactions correspond quite closely with those representing mature plant reactions. Khapli however gives a very typical reaction (figure 17) in that a large number of very small pustules with sharply chlorotic areas are nearly always produced. The rust

Figure 17. Reaction on leaves of mature plants of Khapli to form 15.

Figure 18. Left—reaction of mature plant leaves of Reward to form 21. Right—reaction of mature plant leaves of Reward to form 15.

percentages for the mature plant stage are, therefore, considerably higher than for such a variety as Iumillo or Black Persian. It has been pointed out above that a low percentage of rust is typical of varieties possessing mature plant resistance, regardless of the size of the pustules. In Khapli, therefore the results would indicate a lack of mature plant resistance, i.e., the resistance exhibited in the latter stage is probably exactly the same type of resistance as is shown in the seedling stage.

The results from table 3 may be summarized to some extent in the averages which are shown in the column on the extreme right. Such averages cannot be taken, however, as a complete index of the resistance of a variety. Black Persian, for example, shows about the same average seedling reaction as Pentad, but the former shows a fairly uniform reaction to all forms, while Pentad is highly resistant to some and moderately susceptible to others. The average figure seems to be the most useful for comparing seedling and mature plant reactions. In figure 15 the average results for the seedling reactions, the mature plant reactions, and the percentages of rust of each variety are put in the form of a graph. The varieties are grouped in this graph according to the magnitude of the difference between the seedling and mature plant reactions. The group on the left, from Garnet to Iumillo, show almost identical reactions in the two stages, and are arranged as a group in order of resistance, Garnet being the most susceptibile and Iumillo the most resistant. The remaining group of varieties are arranged in order of the magnitude of the difference between the average reactions in the two stages. In Reward we have the smallest difference, and in Acme the greatest difference. Neglecting the percentage columns, we would classify the entire group on the right as possessing some degree of mature plant resistance. As pointed out previously, however, the evidence is not very definite in the case of Reward. It is evident from the remainder of the group that with plants showing mature plant resistance, there is a very sharp falling off in the percentage of rust. In the group from Black Persian to Hope, the percentages are very small indeed. This is in line with any theory to account for mature plant resistance from the morphological or functional standpoint, especially any type of resistance which hinders the entrance of the infection hyphae. When infection does take place the pustules developed may be fairly large but they are necessarily few in number.

If low percentages of rust indicate mature plant resistance, the varieties, Vernal and Iumillo, in the group to the left in figure 15, both possess mature plant resistance. On account of the high percentage of rust on the Khapli, it is quite out of line with the varieties on either side. The Khapli result, however, as pointed out above, is exactly what we would expect in a variety whose resistance in the later stage is identical with that in the seedling stage. In the same way, the low percentage of rust shown by Vernal and Iumillo are indications of a mature plant type of resistance, the presence of which is masked by the high degree of seeding resistance which continues throughout the life of the plant.

Regional Resistance

In many mature plants different reactions occur on different parts of the same plant. "Regional resistance" seems to be the most suitable term to apply to this phenomenon. The heaviest rusting on a nearly mature plant is, in general, on the regions just above the nodes and on that section of the neck or culm proper, which last emerges from the sheath of the uppermost leaf. This is illustrated in figures 16, 19 and 22. Figure 16 shows the reaction of stems of the variety Quality in the mature stage, to form 38. This variety is resistant to form 38 in the seedling stage, but in the mature stage, certain parts of the plant become very susceptible. The three stems to

Figure 19. Reaction on stems of Marquis wheat to form 50.

Figure 20. Reaction of seedling leaves of Quality wheat to form 38, left, and form 50, right.

the left show a heavy reaction just above the node, the reaction becoming progressively lighter from the node up to the base of the leaf. The smallest stem is a portion of the neck, and from the photograph, it is obvious that the infection here is again quite heavy. The three stems to the right are

slightly enlarged portions of the three on the left. They bring out more clearly the contrast between the heavy infection on the neck and the light infection on the upper part of the leaf sheath. As was stated above, in the seedling stage, Quality gives a 2 reaction to form 38. This agrees quite well with the reaction in the mature plant stage on the leaf sheaths (figures 20 and 21) but it will be seen that a much heavier reaction can be obtained on other parts of the plant.

Figure 19 shows the reaction of Marquis to form 50. The three stems to the left again show very heavy pustules just above the nodes, the pustules gradually becoming smaller higher up on the leaf sheaths. The three stems to the right are enlarged portions of the stems on the left. Marquis in the seedling stage gives a 2- reaction to form 50 and is therefore considered resistant to this form. The reactions on the stems shown here, however, prove that very much heavier reactions can be obtained on certain portions of the mature plant than on seedling leaves.

Figure 22 illustrates the mature plant reaction of Marquis to form 53 to which it gives a $2\pm$ reaction in the seedling stage. Here, again, the seedling reaction is obtained on leaf sheaths and leaves only, as the nodes and necks show much heavier infection. In the above three cases, photographs of leaf reactions have not been shown, as the reactions on the leaves are identical with those on the upper part of the leaf sheaths. This similarity between the seedling reaction and that on the leaves of the mature plant is demonstrated in figures 20 and 21. If anything, the mature plant leaf reaction is slightly more of the resistant type than that of the seedling leaf.

The existence of a regional type of resistance, in some varieties, is extremely interesting when considered in relation to any theories that may be advanced to explain the nature of resistance. A strictly morphological type of resistance, based on the relation between the schlerenchyma and chlorenchyma bundles, would be expected to give the opposite effect to that shown here. According to the results obtained by Hursh (*7*) and Hart (*5*) we should not expect to find either morphological or functional resistance in Marquis. If the resistance is physiological we have to assume an unequal distribution in the plant of the substance or substances responsible for resistance, or an unequal influence in different portions of the plant of another factor super-imposed upon the physiological factors. The study of regional resistance is important, therefore, in that it may give some clue leading to the discovery of the exact nature of physiological rust resistance. Its main interest at the present time is in demonstrating that the reaction of a variety in the seedling stage is not necessarily a criterion of its reaction in the mature plant stage, even if there is no development of a mature plant type of resistance.

Bearing on Functional Resistance

It has been pointed out above that the evidence gathered on mature plant resistance supports in general the theory of functional resistance advanced by Hart (*5*). By genetical studies, it has been shown that mature plant resistance is inherited in a relatively simple manner, which is indirect evidence as to the simplicity of its nature. Hart (*5*) points out that there is

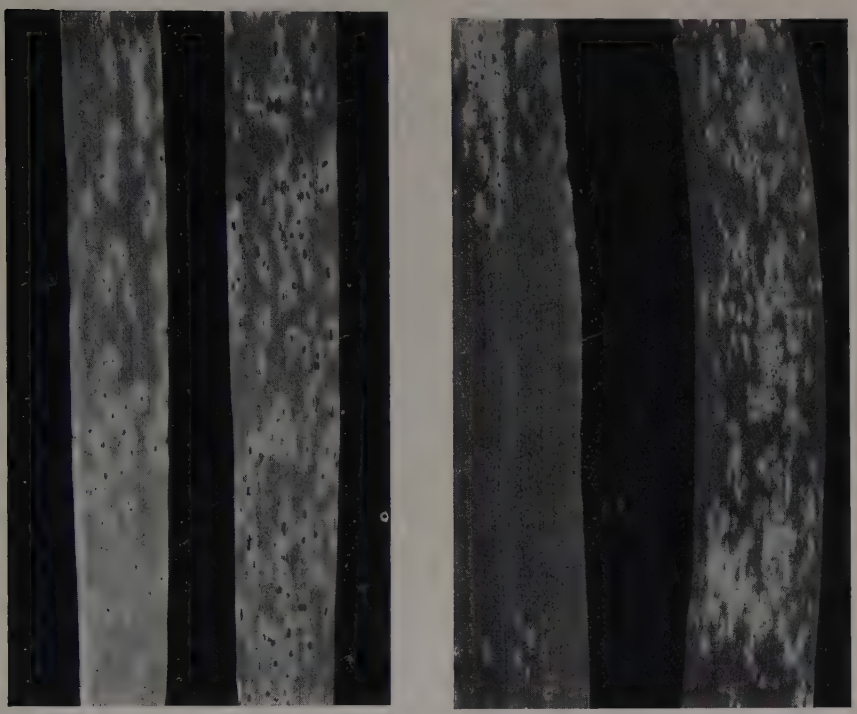

Figure 21. Reaction of mature plant leaves of Quality wheat to form 38, left, and form 50, right.

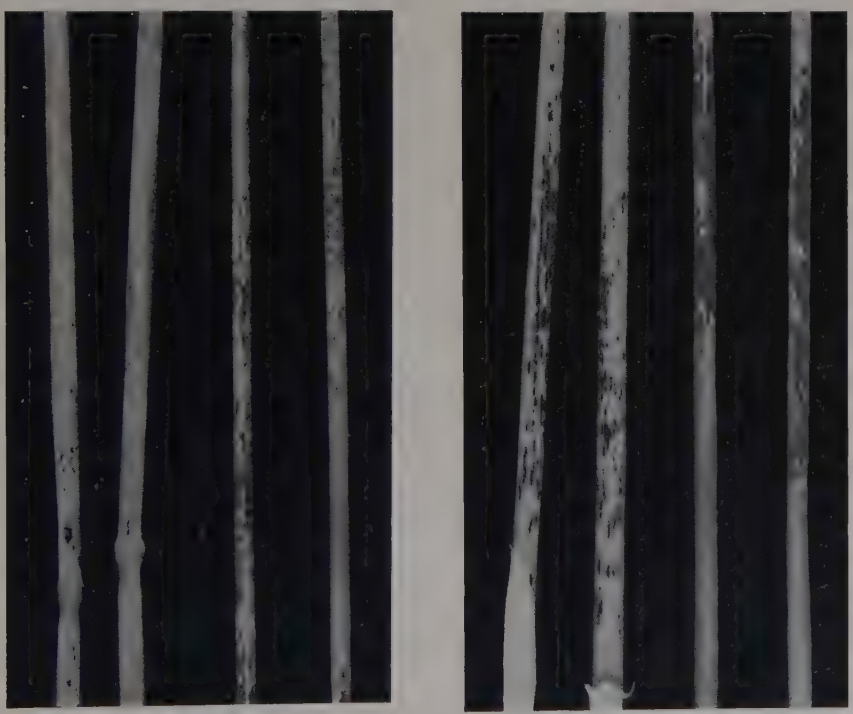

Figure 22. Reaction of stems of Marquis wheat to form 53.

no necessity for assuming the development of another type of resistance. viz., mature plant resistance, as this type may be explained on the basis of stomatal behaviour. Her assumption that a similar stomatal behaviour obtains in the seedling and mature plants seems to have been fairly well demonstrated. She has pointed out, however, that the stomata of mature plants are less sensitive than those of seedlings, and that the relative difference in sensitivity between resistant and susceptible varieties is greater in the mature plant stage than in the seedling stage. The development of such differences is, therefore, if we accept the theory of functional resistance, the development of mature plant resistance, and the two views are quite in accord.

There are, however, a few facts embodied in our results which are difficult to explain on the basis of functional resistance. In the first place, the variety Khapli, which in stomatal behaviour is very similar to Hope and Pentad, gives usually a high percentage of infections. Figure 17 illustrates the typical mature plant leaf reaction of Khapli obtained in our experiments. Similar reactions have been observed in the field. It is difficult to see how similar stomatal behaviour in Khapli, Hope, and Pentad would give such dissimilar results.

It was also noted in our experiments that a variety such as Pentad, which is suceptible to a given form in the seedling stage, would, when tested to this form in the mature plant stage, show not only a low percentage of rust, but also very small pustules. It is difficult to understand how stomatal behaviour can effect the pustule size as well as the number.

Summary

1. The purpose of this study was to obtain more complete information on the reactions of wheat varieties as seedlings, and as fully grown plants, to different physiologic forms of stem rust.

2. Fourteen varieties ,varying from almost complete susceptibility to very high resistance, were tested to 16 physiologic forms for their reactions in the mature plant stage. These results were compared with the corresponding seedling reactions.

3. On the basis of the results obtained, the varieties were divided into three groups. (1) those in which there was almost perfect agreement between the seedling and mature plant reactions, (2) those in which there was a decided lack of agreement between the seedling and mature plant reactions, and (3) a group intermediate between (1) and (2) in which there was imperfect agreement.

4. In group (1) were placed Garnet, Marquis, Quality, Vernal, Khapli and Iumillo; in group (2) Hope, H-44-24, Pentad, Acme, and Black Persian; in group (3) Reward, Kota, and Marquillo.

5. Group (3) contains the varieties in which the presence of mature plant resistance is considered to be definitely established. In group (1) the varieties, Vernal and Iumillo, show close agreement in the reactions of the seedling and mature plants, but the low percentage of rust which develops on these varieties in the mature stage indicates that they too possess mature plant resistance.

6. The resistance which develops in the varieties of group (3) as they approach maturity is explained on the basis of the development of a type of resistance which is different from that observed in the seedling stage.

7. Varieties possessing mature plant resistance reacted fairly uniformly in the mature plant stage to the 16 different physiologic forms. This is an indication that plants possessing this type of resistance will, in general, be resistant to all forms, and, consequently, from the practical standpoint this resistance is of greater importance than seedling resistance.

8. All the varieties tested, especially Marquis and Quality, showed a tendency, in the mature stage, to rust more heavily in certain regions than in others, particularly above the nodes and on the culms between the uppermost leaf and the head. For this phenomenon the term "regional resistance" is suggested.

9. The results obtained are discussed in relation to theories concerning resistance, especially with that of functional resistance, believed to be due to stomatal behaviour. It is shown that, in general, the results support the theory of functional resistance, but that there are a few facts which are difficult to explain on this basis.

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